Responses of Benthonic and Nektonic Organisms, and Communities, to Severe Hypoxia on the Inner Continental Shelf of Louisiana and Texas

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Abstract

We have, over the course of 16 years, accumulated considerable information on the responses of benthonic and demersal organisms to hypoxia (≤ 2 mg/l dissolved oxygen) via direct diver observations, remotely operated vehicle (ROV) video systems, and by sample collection using benthic cores and grabs. As might be expected, the responses of the fauna vary, depending on extent of oxygen depression. In a progressive decrease from 2.0 to about 0.2 mg/l, we have observed progressive disappearance of motile organisms (fish, cephalopods, and crustaceans), to pronounced stress behavior of benthonic organisms incapable of escape, to emergence of deep burrowing benthonic organisms from their burrows, to death of these organisms. At near 0.2 mg/l, the sediment becomes black and sulfur-oxidizing bacteria form "cottony" mats on the sediment surface. At 0.0 mg/l there is no sign of aerobic life, only black sediments.

Episodic hypoxic/anoxic stress may result in temporary destabilization of the benthic assemblage. Evidence suggests that the community recovers to its former diversity and abundance. Repeatedly stressed communities, however, have low diversity, no species with direct development, a few highly tolerant species, low biomass and limited recovery following abatement of hypoxia.

Introduction

Hypoxia (≤ 2.0 mg/l of dissolved oxygen [D.O.]) and anoxia (0.0 mg/l D.O.) occur in many localities (see Tyson and Pearson 1991 and Diaz and Rosenberg 1995, for reviews). In most cases the data generated by studies of hypoxia have reported reduced abundances of benthic fauna and/or the absence of nektonic fauna. There are, however, relatively few studies documenting the effects on these organisms as the oxygen concentration decreases from normoxic to below 2.0 mg/l and continues to decrease toward anoxia. Jorgensen (1980) and Stachowitsch (1991), using scuba, documented behaviors of benthonic organisms during the onset of anoxia, including stress behavior of actiniarians (anemones), ophiuroids (brittlestars), gastropods and bivalves.

In the northwestern Gulf of Mexico (defined here as the Louisiana coast west of the Mississippi Delta and the Texas coast north of Matagorda Bay), prior to 1979, there were a few published reports of dead organisms being collected by trawl or seen by divers (Harper et al. 1981, 1991), and there were anecdotal reports of shrimp fishermen avoiding large areas because nothing was being caught, but no systematic studies had been conducted.

Methods

The behaviors of benthic infauna and epifauna, and demersal nektonic organisms, were observed directly by scuba divers, and by "flying" ROV's. The responses of benthic communities to hypoxia and anoxia were determined by collecting benthic samples using diver-operated, or remotely operated, grab samplers and cores. In addition to direct observation, divers used Nikonos cameras to obtain wide angle photographs and macro-photographs, and the ROV excursions were documented on videotape via electronic signals received from the on-board cameras. These observations and photographic records were made principally during two long-term studies. The first occurred off Freeport, Texas, during a 7-year (1977–1984) study of the macrobenthos, and the second occurred off Cocodrie, Louisiana, during a 5-year (1989–1993) period in which 1-week cruises were made each summer on the Louisiana continental shelf.

Results

In June 1979, during a study of the macro-benthos off Freeport, Texas, divers reported seeing apparently dead infaunal organisms lying on the bottom amidst various sized patches of "cottony" material (probably the sulfur-oxidizing bacterium Beggiatoa); the divers also reported smelling hydrogen sulfide in the bottom water (Harper et al. 1981, 1991). Pavella et al. (1983) simultaneously collected virtually no nekton in the area. Data collected along cross shelf transects indicated the "dead" water extended from about 6-m depth out to about 30-m depth, a cross-shelf distance of 50 km (Harper et al. 1981; Pavella et al. 1983). During, and immediately following, the event, infaunal abundances decreased to the lowest levels reported during the 7-year (1977–1984) study. The deeper study site (21-m depth) recovered quickly to pre-hypoxia conditions (Harper et al. 1991) At the shallower site (15-m depth), however, the benthic community was apparently destabilized, because a succession of dominance occurred in which one species became numerically dominant for 1 to 3 months, then was replaced by another domin-ant. This process continued for almost 2 years until the spionid polychaete Paraprionospio pinnata regained its pre-hypoxia dominance (Harper et al. 1991).

Detailed studies of hypoxia began off Louisiana in 1985 and continue to the present (Rabalais and Harper, 1991, 1992; Rabalais et al. 1991, 1992, 1994a, b; 1996, in press). These studies have documented that up to 18,000 km2 of the Louisiana continental shelf may be impacted by hypoxic/anoxic bottom water. Week-long late summer cruises off Louisiana from 1989 through 1995 have documented several stages of hypoxia/ anoxia, ranging from hypoxia onset to virtual absence of oxygen and the presence of hydrogen sulfide in the water column. These observations have led to the creation of a step-wise effects diagram (Figure 11). Above 2.0 mg/l (normoxia) divers occasionally observe fish, but fish, squid, and large mobile bottom-dwelling organisms are routinely seen during ROV tows (Figure 12). Another characteristic of normoxic water is that it is generally turbid and visibility is limited. As the oxygen level decreases from 2.0 to around 1.5 mg/l the mobile organisms usually disappear. Very often the turbidity in the water decreases. Further reduction from 1.5 to 1.0 mg/l causes stress behavior in smaller bottom-dwelling organisms; crabs and sea stars climb on top of high points, brittlestars emerge from the sediment and use their arms to raise their disks off the substrate, burrowing shrimp emerge from the bottom, snails move about the bottom with their siphons directed upward, large burrowing worms emerge from the substrate (Figure 13). All these actions are taken to position the organisms' ventilation mechanisms (gills, siphons, etc) above the microenvironment at the sediment-water interface where the hydrogen sulfide concentration may be increasing. At oxygen levels of 1.0 to 0.5 mg/l the sediment surface develops "fairy rings" of thin strands of bacterial filaments that appear to expand outward leaving black sediment in the center of the ring (Figure 14). At this stage, even the most tolerant burrowing organisms, principally various types of worms, emerge partially or completely from their burrows and lie motionless on the bottom (Figure 15). Often these organisms can be revived if placed in oxygenated water; several different motionless, and apparently dead, species have been collected in jars on the bottom, returned to the surface and placed in aerated water, and have revived within a half hour. As the oxygen concentration decreases from 0.5 toward zero, bottom organisms die. They do not, apparently decompose rapidly, because their bodies continue to litter the bottom (Figure 16). The absence of large scavengers is also evidenced by the fact that the corpses remain on the bottom and are not eaten. At 0.0 mg/l the sediment becomes almost uniformly black and there is no sign of life; even the strands of the sulfur-oxidizing bacterium Beggiatoa are absent.

Discussion

One of the principal problems associated with hypoxia and anoxia in the marine environment is that the effects on the benthonic and nektonic communities usually cannot be observed directly; the effects must be inferred via reductions in trawl catches or reductions in collected bottom-dwelling organisms. Without the visual impact of stressed, dying, or dead organisms littering the bottom, the effects of reduced oxygen do not generate the same level of consternation that would occur if the same type of catastrophe occurred on land. We suggest that if, for two to three months each summer, dead animals were strewn over 18,000 km^2 of land in Missouri or lowa, people would rightly be upset, and that efforts would be immediately undertaken to correct the situation. Those in agricultural states who depend on soils for their livelihood must realize that worms in the marine environment serve the same function that earthworms do on land; they burrow into the soil, cause mixing, and at the same time allow oxygen to penetrate to deeper levels than would be possible without them. The worms, both terrestrial and marine, contribute greatly to increased overall productivity of their respective habitats.

It is generally accepted that the continental shelf of Louisiana is impacted by hypoxia almost annually, but it had been assumed that occurrences off Texas were infrequent to rare. Studies of the benthos off Freeport, Texas, revealed that hypoxia occurs more frequently off the upper Texas coast than had previously been believed. During the 7-year study off Freeport, Texas, there were two confirmed events of D.O. decreasing below 2 ppm, and three other suspected incidents; if these latter occurred, the events were fairly short-lived and were missed due to the schedule of sampling cruises. Because of the limited area being sampled we do not know the area affected during the catastrophic 1979 event. If, however, as we suspect, the hypoxic water mass was imported from the Louisiana shelf, and extended offshore to at least 28 km, an area of at least 5,400 km^2 was affected along the upper Texas coast. The other event(s) was (were) fairly short-lived and probably had minor effects. The shallower site benthic community was apparently destabilized by the hypoxic event and required about two years to return to pre-event conditions.

The Texas experience is in contrast to the conditions that exist on the Louisiana shelf. The benthos off Louisiana are subjected to hypoxia almost annually, and the hypoxia often extends over 3–4 months. Thus the benthos rarely, if ever, attains a climax community. Rather, the community is grossly reduced, or eliminated, annually and must be reestablished following break-up of the conditions producing hypoxia. This prevents establishment of a climax community.

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